

Drought generates large, long-term changes in tree and liana regeneration in a monodominant Amazon forest

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31 Abstract

32 The long-term dynamics of regeneration in tropical forests dominated by single tree species remains
 33 largely undocumented, yet is key to understanding the mechanisms by which one species can gain
 34 dominance and resist environmental change. We report here on the long-term regeneration
 35 dynamics in a monodominant stand of *Brosimum rubescens* Taub. (Moraceae) at the southern
 36 border of the Amazon forest. Here the climate has warmed and dried since the mid-1990's. Twenty-
 37 one years of tree and liana regeneration were evaluated in four censuses in 30 plots by assessing
 38 species abundance, dominance, and diversity in all regeneration classes up to 5 cm diameter. The
 39 density of *B. rubescens* seedlings declined markedly, from 85% in 1997 to 29% in 2018 after the
 40 most intense El Niño-driven drought. While the fraction contributed by other tree species changed
 41 little, the relative density of liana seedlings increased from just 1% to 54% and three-quarters of
 42 liana species underwent a ten-fold or greater increase in abundance. The regeneration community
 43 experienced a high rate of species turnover, with changes in the overall richness and species
 44 diversity determined principally by lianas, not trees. Long-term maintenance of monodominance in
 45 this tropical forest is threatened by a sharp decline in the regeneration of the monodominant species
 46 and the increase in liana density, suggesting that monodominance will prove to be a transitory
 47 condition. The close association of these rapid changes with drying indicates that monodominant *B.*
 48 *rubescens* forests are impacted by drought-driven changes in regeneration, and therefore are
 49 particularly sensitive to climatic change.

50

51 **Keywords:** drought • regeneration dynamics • saplings • seedlings • lianas.

52

53 Introduction

54 Tropical forests are renowned as being global centres of tree species richness and diversity
 55 (Connell et al. 1984; Gentry 1988). In general, tropical forests are also hyper-diverse at the local,
 56 community scale, with one hectare having as much as 30 times more tree species than an equivalent

57 area in temperate forests (e.g., Gentry 1988; Condit et al. 1996; Torti et al. 2001). Such high alpha
 58 diversity typically pertains across the most extensive tropical forests of all in Amazonia (e.g., ter
 59 Steege et al. 2003), yet for some tropical forests the rule of high alpha-diversity does not hold.
 60 Across the tropics, several studies have reported ‘monodominant’ mature forests even on well-
 61 drained soils, in which one species may comprise from 50% to as much as 100% of the individuals
 62 and the total biomass (Connell and Lowman 1989; Marimon et al. 2001a; Peh et al. 2011b).

63 Several researchers have attempted to identify factors and mechanisms that enable a single
 64 species to reach and maintain monodominance in the tropics (e.g., Connell and Lowman 1989; Hart
 65 1990; Torti et al. 2001; Marimon and Felfili 2006; Marimon et al. 2008, 2012, 2014; Peh et al.
 66 2014; Nascimento et al. 2017; Elias et al. 2018). Peh et al. (2011b) discussed a total of eight
 67 hypotheses that have been proposed to explain the origin and maintenance of monodominance in
 68 tropical forests. They concluded that a variety of mechanisms likely interact to induce a species to
 69 attain monodominance locally, even when that species also grows in similar environmental
 70 conditions in adjacent mixed forests which have much greater tree diversity.

71 Meanwhile, it has long been appreciated that disturbance regimes can have a strong impact
 72 on tropical forest diversity; Connell’s ‘intermediate disturbance’ hypothesis (Connell 1978), for
 73 example, suggests that there is an optimal level of disturbance frequency and intensity above and
 74 below which species diversity declines. Indeed disturbance regimes appear to be intimately
 75 associated with the phenomenon of monodominance (Tovar et al. 2019). Thus, while Ibanez and
 76 Birnbaum (2014) observed that monodominance can occasionally be a non-persistent state that
 77 occurs after severe disturbances (‘early successional monodominance’), one of the factors most
 78 often hypothesised as responsible for favouring a species to reach monodominance is a long-term
 79 lack of large-scale disturbances (Connell and Lowman 1989; Hart 1990; Marimon et al. 2012). In
 80 this situation, species whose seedlings are able to grow under deep shade, and which also have high
 81 parental survivorship and potential to dominate canopies are expected to gain a long-term
 82 advantage. In all, multiple related biological traits and environmental characteristics are likely to be

83 responsible for helping a species develop a monodominant state, including low gap formation
 84 frequency, strong interspecific competition, high parental survivorship and high survivorship under
 85 strong shading, litter characteristics, large seed size, and masting events (i.e., massive, infrequent
 86 seed production in regional synchrony with trees of the same species) (Connell and Lowman 1989;
 87 Hart 1990; Torti et al. 2001; Marimon and Felfili 2006; Peh et al. 2011b; Marimon et al. 2012; Hart
 88 2012; Read et al. 2017; Henkel and Mayor 2019).

89 Evidently then most of the factors and mechanisms invoked in explanations of
 90 monodominance may be best evaluated through examining species regeneration (Connell and
 91 Lowman 1989; Read et al. 2017). For example, if diversity in tropical forests is normally
 92 maintained by compensatory mechanisms that benefit rare species (Connell et al. 1984), then
 93 monodominance may occur when regeneration mechanisms uncharacteristically instead favour
 94 common species and tree diversity remains low. More generally, evaluation of long-term
 95 regeneration dynamics should be able to determine whether changes in diversity occur in
 96 conjunction with changes in disturbance mechanisms, such as droughts, logging and anthropogenic
 97 climate change – all of which impact tree mortality, recruitment, carbon sequestration and species
 98 composition in Amazonia (Phillips et al. 2009; Costa et al. 2010; Brien et al. 2015; Meir et al.
 99 2015; Feldpausch et al. 2016; Esquivel-Muelbert et al. 2019). Yet studies of the stand dynamics of
 100 monodominant forest regeneration are difficult, extremely few and, so far have relied on single
 101 census inventories or short-term monitoring (c.f., Hart 1995; Marimon et al. 2012; Valverde-
 102 Berrantes and Rocha 2014).

103 As well as understanding species regeneration processes, exploring the ecological
 104 interactions between trees and lianas is also essential for understanding how tropical forests
 105 function (Caballé and Martin 2001; Comita et al. 2007). Lianas not only compete effectively with
 106 trees for water, light, space and nutrients (e.g., van der Heijden and Phillips 2009), but by
 107 contributing to gap formation they can accelerate processes of species substitution and forest
 108 dynamics (e.g., Phillips et al. 2005; van der Heijden and Phillips 2009; van der Heijden et al. 2013;

109 Magnago et al. 2017). Since lianas can grow almost ten times faster than trees during the dry
 110 season, they can also have a competitive advantage in forests subject to strongly seasonal
 111 environments (Schnitzer and Bongers 2011). If extreme events of drought and high temperature
 112 become more frequent (Fauset et al. 2012; Boisier et al. 2015) such climate changes could therefore
 113 drive large-scale increases in lianas. Indeed, the recent increases in Amazonian dry season intensity
 114 (e.g. Malhi et al. 2009; Gloor et al. 2013; Feldpausch et al. 2016; Esquivel-Muelbert et al. 2019)
 115 might help explain the increase in liana dominance that has been reported from many forests (e.g.,
 116 Phillips et al. 2002; Nepstad et al. 2007; van der Heijden et al. 2013).

117 In Amazonia, one of the few species capable of attaining monodominant status is *Brosimum*
 118 *rubescens* Taub., a canopy tree in the Moraceae. *Brosimum* stands covered areas of up to 5,000
 119 hectares, especially, until recently, in the transition zone between the two largest biomes in the
 120 continent, the Amazonian Forest and the Cerrado (savannah), in the Brazilian states of Mato
 121 Grosso, Pará and Tocantins (Marimon et al. 2001a, b, 2008, 2012, 2014). With large-scale regional
 122 deforestation for pasture and soya agriculture, and logging focussed on this species for use as fence-
 123 posts for pastures, today the *Brosimum*-dominated forests are few and small, restricted mostly to
 124 indigenous reserves and forest reserves on large farms. Typically the remaining patches of this
 125 unique habitat lack any management plan or any type of conservation action (Marimon et al. 2001a,
 126 b, 2008). Where *Brosimum* monodominant forests still occur they are situated in an area of
 127 particularly rapid recent climate change, and where future climates are expected to be warmer and
 128 drier (Costa et al. 2010, 2019). This climate change may already be inducing a regional acceleration
 129 of forest dynamics (Marimon et al. 2014; Elias et al. 2018), which could have the potential to
 130 radically alter the regeneration dynamics and liana dominance of the remaining intrinsically slow
 131 nutrient turnover monodominant systems (Torti et al. 2001; Peh et al. 2011a, b).

132 In the present study, we evaluated richness, species diversity and change of the regeneration
 133 in a monodominant *B. rubescens* forest over a 21-year period in the transition zone between the
 134 Cerrado and the Amazonian biomes. Because adult tree mortality in this patch has increased

markedly over recent years, our main prediction was that the density of young individuals of *Brosimum* would have declined over time, while species diversity increased. We evaluated regeneration of woody plants over time and tested the hypotheses that after severe droughts density declines, and species composition changes. By including lianas as well as trees in our forest regeneration censuses we were able to investigate the role of lianas in forest regeneration. To our knowledge the present study represents by far the longest-running assessment of regeneration in monodominant forests to date anywhere in the tropics, and is the first attempt in such systems to explicitly account for the long-term regeneration of woody lianas as well as trees.

Materials and methods

Study site

The study was conducted in *Brosimum rubescens* monodominant forest located at 14°50'S and 52°10'W in a patch of about 1,000 ha inside an area bigger than 8,000 ha of the Vera Cruz Farm legal reserve. *Brosimum* dominates the forest biomass and comprises more than half of all individuals (Marimon 2005; Marimon et al. 2001a, 2014). This forest has been monitored since 1996 by the senior author using permanent. The climate is type Aw, according to Köppen's classification, with a dry season from May to September and five to six months of rain (Alvares et al. 2013), leading to maximum cumulative water deficits (MCWD, Aragão et al. 2007) exceeding 400 mm in most years. Mean annual precipitation is 1432 mm and mean annual temperature 25°C. Severe droughts (here considered as total annual precipitation below 1,000 mm and with MCWD above 640 mm year⁻¹), were experienced in the study area in 2007-2008 and 2015-2016 (Feldpausch et al. 2016; Jiménez-Muñoz et al. 2016; Rifai et al. 2018), with a general trend of markedly increasing temperature and declining precipitation (more negative MCWD values) over the past 22 years (Fig. 1).

161 Data collection

162 In July 1997, within a permanent 1 ha plot, we established two parallel transects (10 m x 150 m) 10
 163 m away from each other, each of which followed the gentle relief of the landscape so as to maintain
 164 the same altitude. Each transect was subdivided into 15 contiguous subplots of 10 m x 10 m each,
 165 where we counted and identified to species (or morphospecies) all individuals < 5 cm in dbh
 166 (diameter at breast height). Within these subplots we nested smaller plots to sample vegetation in
 167 different size classes, totaling 30 per class: 1 m \times 1 m (seedlings: height ≤ 30 cm), 2 m \times 2 m
 168 (saplings: > 30 cm to ≤ 60 cm), 5 m \times 5 m (poles or young stems: > 60 cm to ≤ 200 cm) and 10 m \times
 169 10 m (treelets: height > 200 cm and diameter < 5 cm). To evaluate temporal regeneration dynamics
 170 the forest was resampled in July 2002, December 2010 and August 2018, using the same
 171 procedures, and the data from the two transects were grouped for each class. The same botanist and
 172 field leader (BSM) participated in all four inventories to ensure standardized identification of the
 173 species. We consider in the different size classes all species whose stems can reach diameters ≥ 5
 174 cm, including woody lianas and palms.

175

176 Data analysis

177 To characterize the change in moisture stress, we calculated temporal trends in MCWD
 178 (Aragão et al. 2007). MCWD is an annual water deficit metric based only on climatic variables and
 179 for which the starting point each year is defined as the wettest month, when the soil is completely
 180 saturated. Climate data were obtained from the INMET (National Institute of Meteorology)
 181 meteorological station (World Weather Station 83319; inmet.gov.br), located in Nova Xavantina,
 182 Mato Grosso state, 25 km from the study area. Evapotranspiration data were based on Malhi et al.
 183 (2009).

184 We calculate Pielou's evenness and Shannon diversity (H') indices for each regeneration
 185 class (seedlings, saplings, poles and treelets) for each census using the *veganR* package (Oksanen
 186 et al. 2018), both when including (All= all species) and excluding lianas (WL= without lianas) from

187 the analyses. In order to compare the species richness of all regeneration classes among the
 188 censuses, we used sample-based rarefaction curves (Gotelli and Colwell 2001) performed in the
 189 BiodiversityR package (Kindt and Coe 2005), and based on 9999 Monte Carlo permutations.

190 To evaluate changes in the species composition of the regeneration classes among censuses,
 191 we performed a permutation-based test of multivariate homogeneity of group dispersions
 192 (PERMDISP) on each distance matrix using ‘permutest.betadisper’ function in the *vegan* package
 193 (Oksanen et al. 2018). If one of the groups (here surveys) has a significantly higher mean distance,
 194 then this group has more dissimilar assemblages on average and greater beta diversity (Anderson et
 195 al. 2006). Euclidean distance among the groups was estimated in a Principal Coordinates Analysis
 196 (PCoA). The significance and pairwise comparisons of Betadisper’s groups were tested by a
 197 permutational multivariate analyses of variance – PERMANOVA (Anderson 2001; Anderson and
 198 Walsh 2013) based on 9999 permutations. We also performed a PERMDISP to evaluate changes in
 199 the average MCWD and temperature registered in the periods before each census.

200 We tested the spatial autocorrelation on the abundance and richness in plots and subplots
 201 using Mantel Correlogram (Borcard and Legendre 2012) performed in the *ncf* package (Bjornstad
 202 2018). To evaluate patterns in density of individuals in all regeneration classes between censuses
 203 we used repeated-measured ANOVA based in the *stats* package (R Core Team 2018). All
 204 statistical analyses and graphs were performed in software R 3.5.1 at 5% alpha-level (R Core Team
 205 2018).

206

207 **Results**

208 For most size-classes rarefaction curves rapidly saturated (Supplementary Fig. S.1),
 209 indicating that the local woody regeneration community was effectively sampled. No spatial
 210 autocorrelation was detected for any regeneration class in any census. There were notable
 211 differences in diversity between censuses however. In particular, when we consider all species
 212 together, for both the seedling and treelet size-classes, species richness had significantly increased

213 by 2018. Yet once lianas were removed from the analysis, in all four regeneration size classes tree
 214 species richness was maximal in 2002, and had declined substantially by the time of the inventories
 215 conducted after the 2007-2008 drought (2010) and the 2015-2016 drought (2018) (Supp. Fig. S.1).

216 When all regeneration size classes are treated together there was no obvious trend in species
 217 richness (Table 1). However, when we analyzed the data by each size class, we detected a marked
 218 increase in the species richness of seedlings and saplings between 1997 and 2018. Furthermore, in
 219 all regeneration size classes the proportion of liana species and liana abundance increased (Table 1).
 220 The increases in both absolute and relative abundance of lianas were particularly marked among the
 221 seedling and sapling classes, and particularly so in the latter censuses, with lianas contributing less
 222 than 1% of woody plant seedlings in 1997 but more than 50% of all woody plant seedlings by 2018.

223 Overall, the abundance of seedlings and saplings declined over the monitoring period,
 224 especially after the drought events (Fig. 2; Supp. Fig. S.2). This was true whether analyses were
 225 conducted with or without lianas (Fig. 2). Nevertheless, the species richness of treelets ($F= 49.67$,
 226 $P= 0.001$), and the Shannon's diversity of treelets ($F= 28.52$, $P= 0.001$) and seedlings ($F= 7.07$, $P=$
 227 0.006) were all higher after the 2015-2016 extreme drought event, but only significantly so when
 228 lianas are included (Fig. 2). Evenness varied between the regeneration classes, being lower in 2018
 229 for poles (All: $F= 12.56$, $P= 0.001$; WL: $F= 11.99$, $P= 0.002$), higher in 2018 for seedlings (All: $F=$
 230 12.01 , $P= 0.002$; WL: $F= 22.47$, $P= 0.001$) and saplings (All: $F= 6.61$, $P= 0.009$; WL: $F= 13.01$, $P=$
 231 0.001), while for treelets it did not change over the censuses (Fig. 2).

232 While total species richness varied little (Table 1), except for the treelet size class when
 233 lianas were included (cf Fig. 2), there was substantial species turnover through time for all
 234 regeneration classes (Supp. Fig. S.3). For instance, we observed: (1) 13 species in the first survey
 235 that were not observed in the second; (2) 15 in the second that were not observed in the first; (3) 18
 236 in the second not observed in the third; (4) 14 in the third not observed in the second; (5) eight in
 237 the third not observed in the fourth; and (6) 18 species in the fourth survey that were not observed
 238 in the third. This resulted in an average rate of change in species composition of nearly three species

239 per year. Thus, while we find that overall species diversity was remarkably stable, species
 240 composition changed substantially, and this holds whether or not lianas are included in the analysis
 241 (Supp. Fig. S.3).

242 The most abundant species sampled in all regeneration classes in all four surveys were
 243 *Brosimum rubescens* Taub. (Moraceae), *Protium pilosissimum* Engl. (Burseraceae), *Ephedranthus*
 244 *parviflorus* S.Moore (Annonaceae), *Inga heterophylla* Willd. (Fabaceae), and *Myrciaria floribunda*
 245 (H.West ex Willd.) O.Berg (Myrtaceae). Other species, such as *Cheiloclinium cognatum* (Miers)
 246 A.C.Sm. (Celastraceae), *Protium altissimum* (Aubl.) Marchand (Burseraceae), and the liana,
 247 *Anthodon decussatus* Ruiz & Pav. (Celastraceae), were also well represented, but in some surveys
 248 did not appear in all regeneration classes. Among the most abundant species, the only one that
 249 increased in number of individuals in all regeneration classes and in all surveys was the liana
 250 *Anthodon decussatus*. We registered a total of 19 species of lianas in all regeneration classes and all
 251 surveys. Of these 16 increased by between 1 to 2,324 individuals/100 m² from the first (1997) to the
 252 last (2018) survey. Three-quarters of all liana species underwent a ten-fold or greater increase in the
 253 number of individuals.

254 Most of the changes observed for tree seedlings was due to a sharp decrease in the
 255 *Brosimum rubescens* population over time (Fig. 3). There were significantly more *B. rubescens*
 256 seedlings in the first census than in any other, with particularly low densities of seedlings and
 257 saplings by the time of the final two surveys (Fig. 3). Over the 21 year period, the proportion of *B.*
 258 *rubescens* seedlings as a fraction of the total population declined from 82% to 45%. In addition, *B.*
 259 *rubescens* seedlings as a fraction of the whole community declined from 85% in 1997 to just 29%
 260 in 2018. Part of this relative decline of *B. rubescens* seedlings was due to increase in the
 261 regeneration of ten liana species, which had only one seedling species and almost no seedling
 262 individuals in the first census, but represented 53.3% of the community's total seedlings by 2018
 263 (Table 1; Fig. 3). Between 1997 and 2018, the proportion of lianas of the combined regeneration in
 264 the forest increased from 1 to 37% (Table 1), with a significant increase in all regeneration classes

(Fig. 3). The remarkable gain in liana seedling and sapling relative abundance is thus not only because lianas increased greatly, but also because there was in numerical terms an even bigger reduction of *B. rubescens* and other tree species in these classes (Fig. 3).

Discussion

Here we report the first long-term analyses of trends in the recruitment of a monodominant tropical forest. We found unexpectedly large changes, including a dramatic decline in dominance of the smaller size classes of *Brosimum rubescens*, and a compensatory shift towards dominance of the seedling community by lianas. The nature and the timing of the shifts and the length of the observation window is consistent with drought events inducing long-term shifts in the structure and floristic composition of the forest regeneration (seedlings, saplings, poles and treelets), particularly via increases in liana richness and abundance.

Differences in beta diversity over the years indicate that the regeneration component of the monodominant forest has been undergoing a shift in floristic composition, again with lianas playing a key and growing role. Thus the community richness and diversity of the regeneration classes in the forest changed significantly throughout time, especially comparing the first (1997) and last surveys (2018), and this occurred because nine species of lianas entered the community. Regardless of mortality patterns among larger trees (Meir et al. 2015; Elias et al. 2018), these changes in the regenerating cohorts could eventually drive the disappearance of species from the community as the floristic composition of juveniles will shape the woody community that reaches the canopy in coming years (Hart 1995; Schnitzer et al. 2000; Marimon et al. 2012, 2014).

We also find a sharp decline in the density of *Brosimum rubescens* among regenerating taxa. Such declines in principle might be attributable to several internal and external factors, including increases in drought frequency and intensity, air temperature, interspecific competition for resources, and human-induced disturbances among others (Feldpausch et al. 2016; Elias et al. 2018; Esquivel-Muelbert et al. 2019). While our study forest showed no signs of recent human-induced

disturbance nor herbivory or disease outbreaks, it did experience substantial increases in temperature and declines in precipitation (more negative MCWD) especially between 2007 and 2017. Thus, we infer that the observed temporal change in regeneration of *B. rubescens* is associated with the recent, strong and repeated drought events (c.f. Marengo et al. 2011; Boisier et al. 2015; Brien et al. 2015; Feldpausch et al. 2016; Esquivel-Muelbert et al. 2019) that in turn have long-term cumulative effects in diversity and richness of the whole community. Elsewhere, in north-eastern Amazonia, some species studied by Costa et al. (2010) during a seven year experimental drought showed similar rates of mature tree mortality as we reported here for *B. rubescens* regeneration. Observations from our site and elsewhere suggest that drought (1) negatively affects production and survivorship of monodominant species seeds, whose dispersion usually occurs at the dry-season peak, and (2) limits their germination, which occurs in the beginning of the rainy season, as persistent water deficits inhibit germination and so act as a regeneration filter in low rainfall years (Marimon and Felfili 2006). However, it is also possible that numbers at the initial survey (1996) were boosted partly by higher than normal rainfall in years prior to the first sampling (Marimon et al. 2012), or other factors such as interspecific competition may also affect recruitment. However, even if *Brosimum* seedlings were boosted by earlier higher rainfall, we can be sure that this didn't happen again over the subsequent 21 years. Moreover, while reliable weather records locally only date to the 1990s, we know from other records in the oldest weather station of Mato Grosso, dating back to 1911 (Bombled 1976; Silva 2015; INMET 2019) that our monitoring period was climatically exceptional. The precipitation registered in Nova Xavantina in both the 2007 and 2015-16 droughts were unprecedented in terms of low rainfall in the recorded history of the region.

Some studies suggested that intense reproductive investment, mast-fruiting and exceptional seedling survival all tend to characterise monodominant species (Torti et al. 2001; Peh et al. 2011b; Henkel and Mayor 2019). Marimon and Felfili (2006) observed these same characteristics in *Brosimum rubescens*, and also suggested that this species has an episodic recruitment. These

317 authors also observed that in 1997 there was a large seedling bank in the forest, probably originated
 318 from prior mast-fruited events, thus is possible that drought mortality can have disproportionate
 319 impacts on the recruitment capacity of this species particularly if the drought occurs in the same
 320 year as the episodic recruitment. Elsewhere, in a Mediterranean environment, Pérez-Ramos et al.
 321 (2010) observed from a long-term data set and a rainfall exclusion experiment that mast-fruited of
 322 *Quercus ilex* itself declined significantly under drier conditions, leading to negative consequences
 323 for recruitment.

324 Regardless of the cause, the decline in *B. rubescens* sapling density between the second
 325 (2002) and third survey (2010), and between the third and fourth surveys (2018) resulted from a
 326 lack of seedlings to replace individuals in this category, indicating that this species' size structure is
 327 unstable and that the population is declining. Notably, other, earlier studies of Neotropical
 328 monodominant forests found no such evidence for decline of the dominant. Both in a
 329 monodominant forest of *Peltogyne gracilipes* Ducke in northern Amazonia (Nascimento and
 330 Proctor 1997; Nascimento et al. 2014) and a gallery forest in central Brazil (Felfili 1997), the
 331 dominant taxon appeared to have a stable population, with large numbers of individuals in each
 332 class, a high density of seedlings, and a constant proportion among classes through time.

333 In contrast to the performance of our dominant, the density of seedlings of some other
 334 species increased through time. These winners included especially the liana species, which may be
 335 benefiting from the openness of the forest (Schnitzer et al. 2000) recorded in recent years after
 336 increased mortality of adult trees (Elias et al. 2018), but also the tree species *Protium altissimum*,
 337 whose seed production occurs in the middle of the rainy season (Marimon and Felfili 2006) when
 338 the forest is fully hydrated so that even in low rainfall periods seed production is less likely to be
 339 affected. Ultimately though, these species' populations may be controlled by competition from the
 340 monodominant for space and light, since the seedlings of *B. rubescens* are able to establish and
 341 survive under closed canopy. This enables this species to occupy the available understory sites and
 342 grow quickly when a canopy gap forms, suppressing the other competitors by limiting their space

343 and available light (Marimon and Felfili 2006; Hirzel and Lay 2008). The competitive advantage of
 344 some liana species in drier conditions (Cai et al. 2009; Campanello et al. 2016) may lead to the
 345 replacement of *B. rubescens* (as clearly recorded for 2010 and 2018) by other species. Indeed
 346 elsewhere in the tropics, studies clearly show more liana infestation of trees in more seasonal
 347 climates and less rain, and potential for liana growth to be several times more rapid than trees in the
 348 dry season (De Walt et al. 2010; Toledo et al. 2011; Schnitzer and Bongers 2011). In addition to *B.*
 349 *rubescens*, the group of more abundant tree species also declined in number of individuals over the
 350 21 years of study, indicating instability in their regeneration and suggesting that they too may be in
 351 decline as an oligarchy. Consistent with our findings and interpretation that this forest is undergoing
 352 drought-induced shifts in tree species composition, a recent Amazon-wide analysis of trees >10 cm
 353 diameter found that dry-affiliated genera have become more abundant and that small-statured non-
 354 pioneer taxa have decreased in abundance in the last 30 years (Esquivel-Muelbert et al. 2019).
 355 While drought is clearly capable of shifting Amazon tree communities (Costa et al. 2010; Meir et al.
 356 2015), our analysis suggests that some monodominant forests may be particularly vulnerable to
 357 drought-induced shifts in the long-term.

358 The large increase in the proportion of liana seedlings in our forest may also be at least in
 359 part a consequence of changes in regional climate. In particular, the increase in temperatures and
 360 the highly variable precipitation experienced over the last two decades has already impacted
 361 Amazon tree biomass and mortality rates (Phillips et al. 2009; Brien et al. 2015; Feldpausch et al.
 362 2016; Esquivel-Muelbert et al. 2019). This mortality increase may be changing the illumination and
 363 moisture conditions experienced by young plants in the understory sufficiently to favour lianas. The
 364 strong competitive capacity of lianas (Putz 1980; Phillips et al. 2005) contributes to their abundance
 365 in tropical forests, and their ability especially to compete below-ground for scarce water resources
 366 (e.g., Schnitzer 2005) may help to explain a tendency within Amazonia for lianas to be particularly
 367 dominant in some forests with long dry seasons (e.g., Pérez-Salicrup et al. 2001).

368 In our study, by the time of the final survey the proportion of lianas in the total community
 369 of regenerating plants (37%) was greater than expected in mixed tropical forests where lianas
 370 usually account for between 15 and 25% of stems and woody species (Gentry 1991; Condit et al.
 371 1996; Torti et al. 2001; Oliveira et al. 2014). The proportion of lianas in our forest is also higher
 372 than reported from Barro Colorado Island in Panama, where lianas composed 17% of the
 373 individuals ≥ 20 cm in height and < 1 cm dbh (Comita et al. 2007). However, in three surveys
 374 carried out by Marimon (2005) in our forest, adult lianas (dbh ≥ 5 cm) accounted for less than 10%
 375 of the woody individuals, while Nascimento et al. (2007) likewise observed a low density of adult
 376 lianas in a monodominant forest of *Peltogyne gracilipes* in Amazonia. This suggests that the
 377 proportion of lianas in low turnover monodominant forests, like other late successional
 378 communities (Ladwig and Meiners 2010), is generally low. This strengthens the interpretation that
 379 the general increase of liana regeneration observed in our study is related to changes in the
 380 frequency of disturbance caused by drought-induced tree mortality and tree-fall (Marimon et al.
 381 2014; Elias et al. 2018).

382 Elsewhere in Neotropical forests, gains in lianas have also been noted but these reports all
 383 come for mixed forests with higher initial populations of lianas than in the monodominant forests.
 384 A general increase in Amazon liana dominance and density was first reported almost two decades
 385 ago (Phillips et al. 2002), and was linked to the long-term increase in forest dynamics already being
 386 experienced in mature old-growth forests across Amazonia (Phillips et al. 2004). More recent work
 387 has tended to confirm that many neotropical forests have been experiencing a prolonged increase in
 388 liana density and dominance (e.g. Schnitzer and Bongers 2011), but the mechanism(s) responsible
 389 remain unclear. Our study strengthens the case for drought as a driver of long-term increases in
 390 neotropical liana populations.

391 The observed increase in the proportion of lianas may therefore represent an additional
 392 threat to the stability of this forest and to the maintenance of *Brosimum rubescens* monodominance.
 393 This is because lianas alter interspecific competitive relationships by impacting the growth of some

394 tree species more than others (van der Heijden and Phillips 2009). Further, by increasing the rate of
 395 tree fall (Phillips et al. 2005), lianas may create conditions suitable for further expansion and affect
 396 the regeneration and dynamics of woody seedlings (Schnitzer et al. 2000; Restom and Nepstad
 397 2004).

398 In conclusion, we found that changes in the richness and diversity of the forest regeneration
 399 were determined by the liana species. The greatest increase in density was also observed for lianas,
 400 such that during the 21-year study period this guild went from being initially almost
 401 inconsequential, to attaining levels higher than those found in tropical forests with high diversity,
 402 and well above levels reported for monodominant forests elsewhere. This recent increase in lianas is
 403 in line with observations from across Amazonia and beyond, but is considerably more marked here.
 404 This may be because our forest is situated at the climatic margins of Amazonia, where recent
 405 droughts and a long-term increase in temperatures may be especially favourable to lianas. In
 406 parallel, there has been a sharp decline in the smallest size-classes of the monodominant tree
 407 species, *Brosimum rubescens*. If these trends (increase in lianas, hotter and more variable climate,
 408 and decline in *B. rubescens* regeneration) continue, we anticipate that the structure and the floristic
 409 composition of this tropical monodominant forest will experience large changes, potentially
 410 becoming transformed into a mixed forest. Since ongoing land-use change, climatic changes, and
 411 increases in lianas appear to be almost ubiquitous among tropical forests of the Americas, our
 412 results suggest a high level of threat to the survival and maintenance of remaining *Brosimum*
 413 *rubescens* monodominant forests.

414

415 **References**

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Table 1 Total species richness (Sp), proportion of liana species (%L_{sp}) and lianas abundance (%L_{ab}) in relation to total community by years and regeneration size classes in a monodominant forest in Southern Amazonia, Brazil. Note the rapid increase in liana diversity and especially in liana dominance in all regeneration classes. Seedlings: height \leq 30 cm; saplings: $>$ 30 cm to \leq 60 cm; poles or young stems: $>$ 60 cm to \leq 200 cm; treelets: height $>$ 200 cm and diameter $<$ 5 cm.

Regeneration	1997			2002			2010			2018		
class	Sp	%L _{sp}	%L _{ab}	Sp	%L _{sp}	%L _{ab}	Sp	%L _{sp}	%L _{ab}	Sp	%L _{sp}	%L _{ab}
Seedlings	10	10	0.8	15	20	1.7	14	28	23.1	19	53	53.3
Saplings	13	15	0.9	28	18	3.1	18	22	3.2	22	32	16.9
Poles	50	16	6.0	53	9	3.9	43	21	4.4	49	27	10.3
Treelets	52	11	2.7	56	4	0.3	53	21	6.3	62	24	14.7
All	64	11	1.0	63	10	2.3	60	23	13.3	71	24	36.8

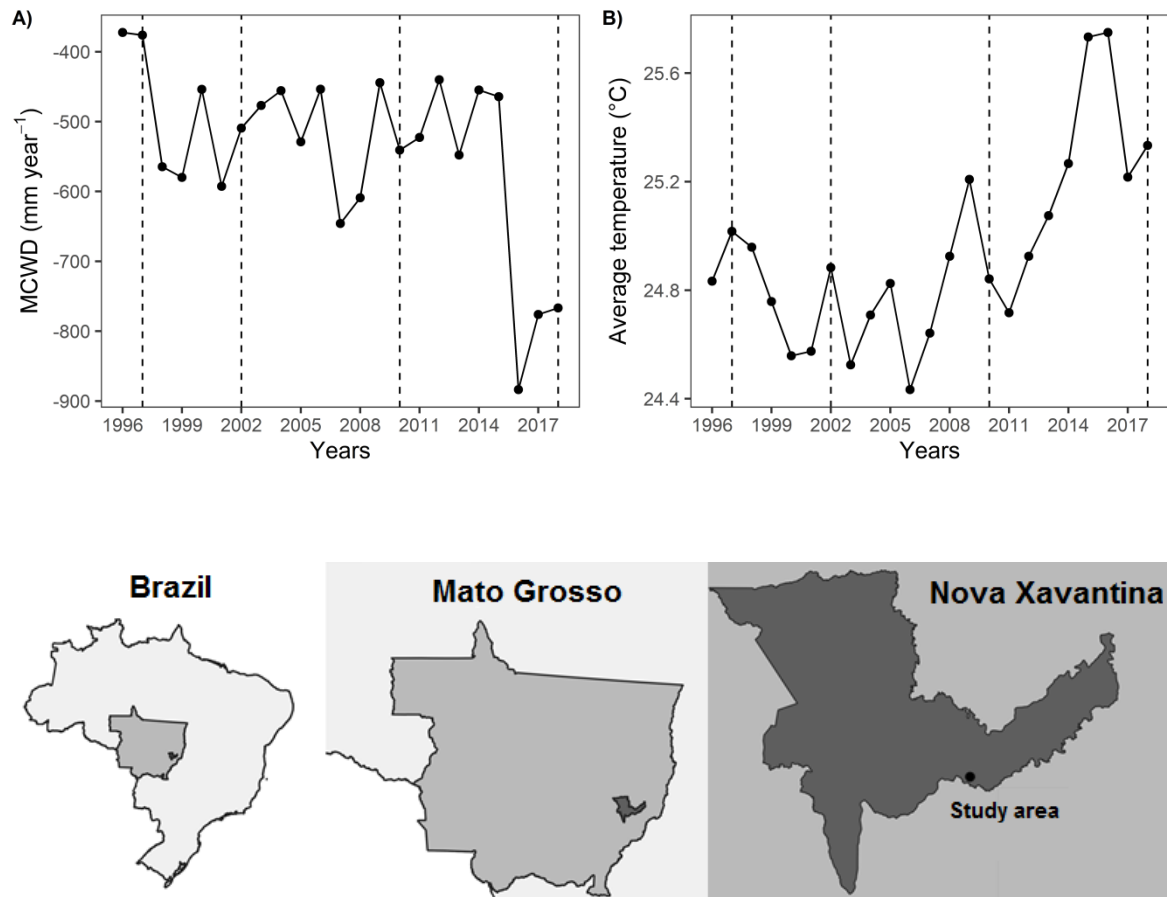


Fig. 1 A) MCWD (maximum climatological water deficit, mm year⁻¹) and B) average air temperature (°C) from 1996 to 2018, with the first month of the dry season (May) representing the beginning of each year's climatic calendar. Precipitation and temperature data were collected at the Meteorological Station (World Weather Station 83319) in Nova Xavantina, Mato Grosso state, 25 km from the study area. Dashed lines indicate the year of each census (1997, 2002, 2010 and 2018).

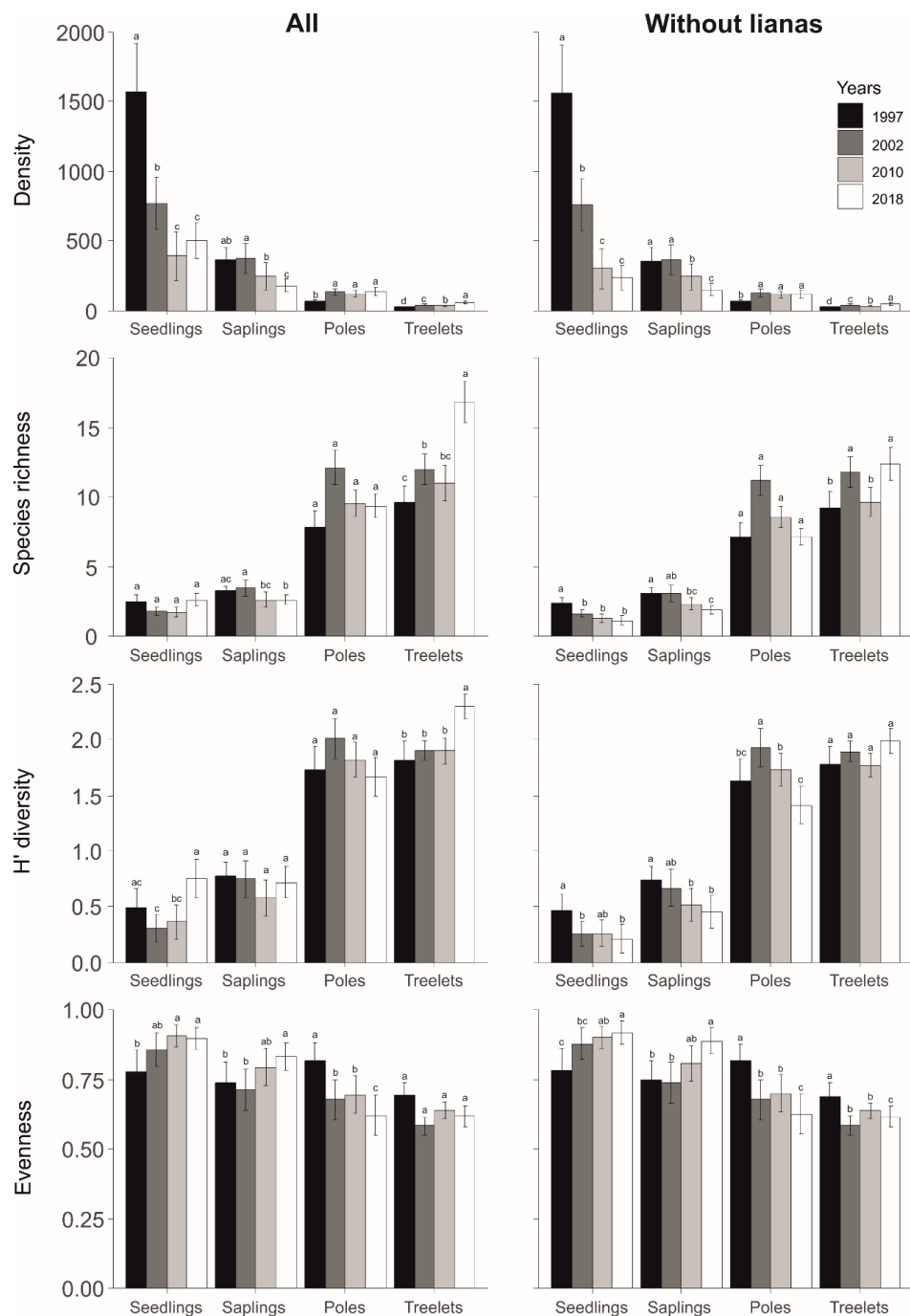


Fig. 2 Average (and confidence intervals) values of the density (100 m^{-2}), species richness, evenness and Shannon's diversity (H') in four regeneration classes (seedlings: height ≤ 30 cm; saplings: > 30 cm to ≤ 60 cm; poles or young stems: > 60 cm to ≤ 200 cm; treelets: height > 200 cm and diameter < 5 cm; $N= 30$ plots per class) in a monodominant forest in Southern Amazonia. Different letters denote significant differences between surveys in each regeneration class (Repeated-Measures PERMANOVA). Note that lianas form a small fraction of woody regeneration early on but become increasingly more important especially in the smallest size-classes.

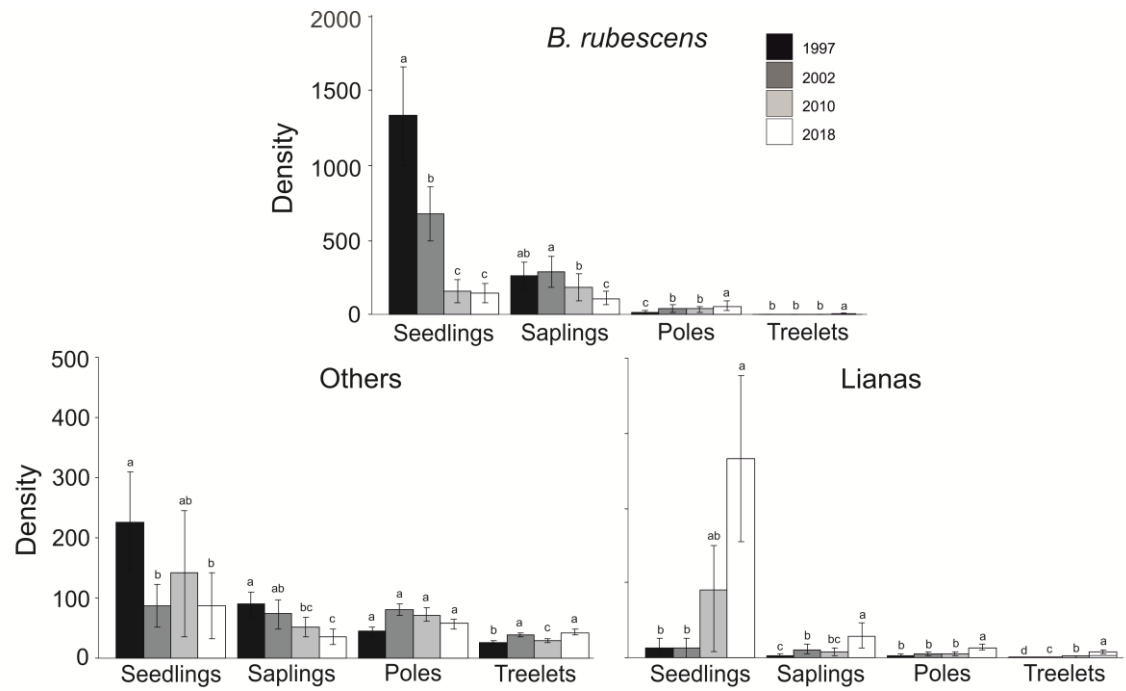
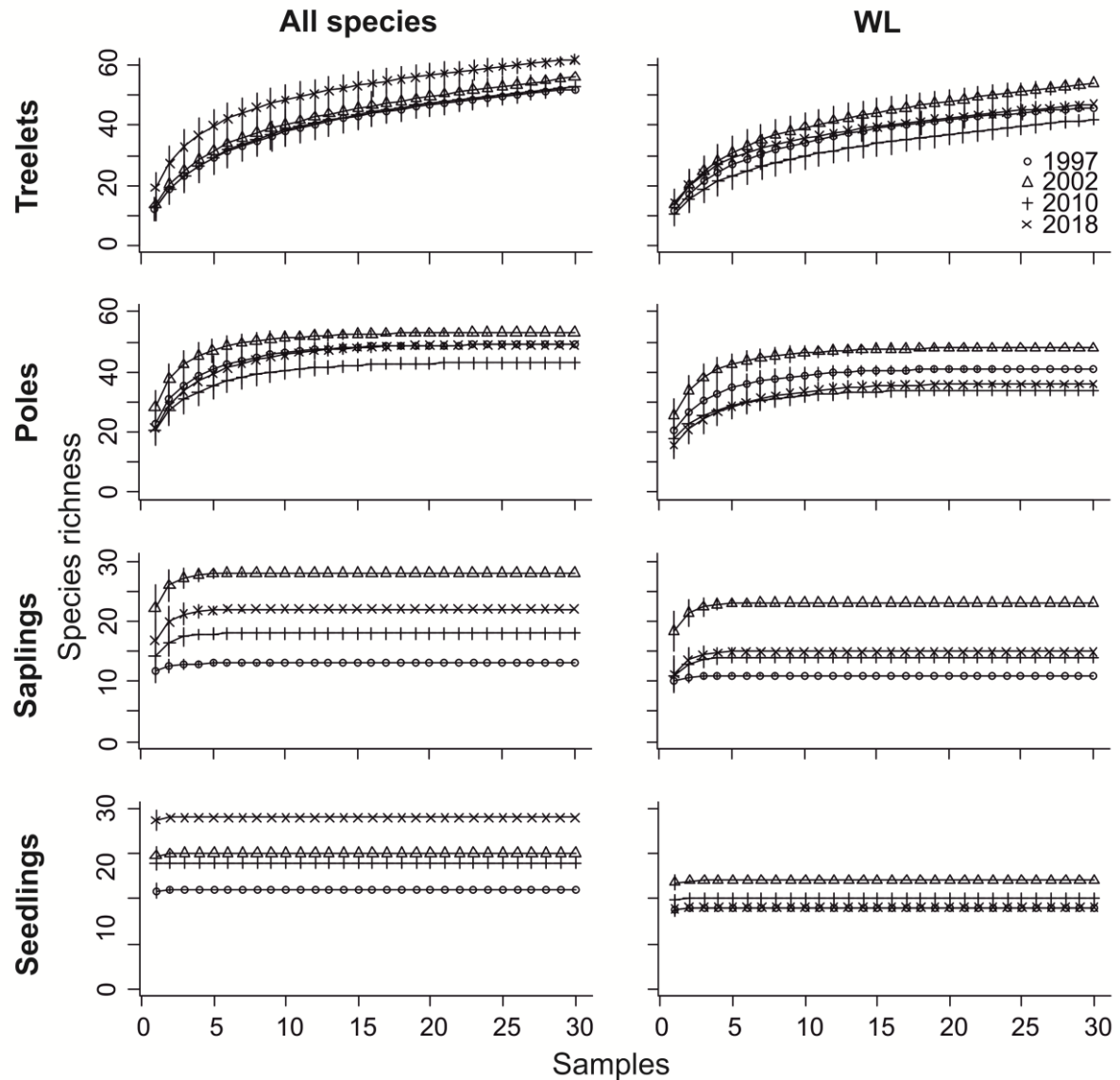


Fig. 3 Average number of individuals and confidence interval of *Brosimum rubescens*, other woody species, and liana-only regeneration in four classes (seedlings: height ≤ 30 cm; saplings: > 30 cm to ≤ 60 cm; poles or young stems: > 60 cm to ≤ 200 cm; treelets: height > 200 cm and diameter < 5 cm; N= 30 plots per class) and four surveys in the monodominant forest in Southern Amazonia, Brazil. Density= average number of individuals per 100 m² plots. Different letters mean significant differences between surveys in each regeneration class (Repeated-Measures PERMANOVA).

806 **Supplementary file 1** related to “Drought generates large, long-term changes in tree and liana regeneration in a
 807 monodominant Amazon forest” (B. S. Marimon, C. Oliveira-Santos, B. H. Marimon-Junior, F. Elias, E. A. de Oliveira,
 808 P. S. Morandi, N. C. C. dos S. Prestes, L. H. Mariano, O. R. Pereira, T. R. Feldpausch and O. L. Phillips)
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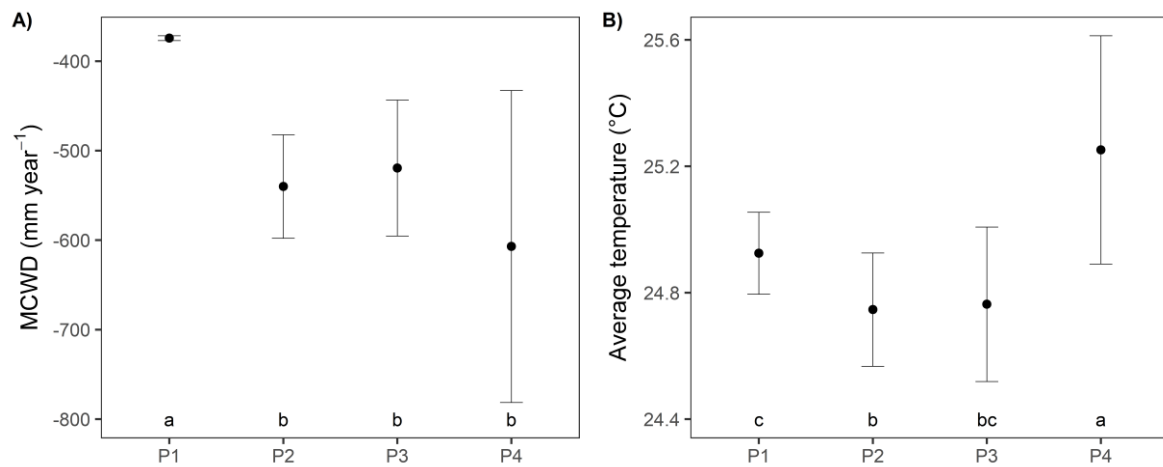


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811 **Supplementary Fig. S.1** Sample-based rarefaction curves for species richness for each census (1997, 2002, 2010 and
 812 2018) and for each regeneration size class (seedlings: height ≤ 30 cm; saplings: > 30 cm to ≤ 60 cm; poles or young
 813 stems: > 60 cm to ≤ 200 cm; treelets: height > 200 cm and diameter < 5 cm) in a monodominant forest in Southern
 814 Amazonia, Brazil. The level of probability of the confidence intervals is 95%. WL= without lianas.

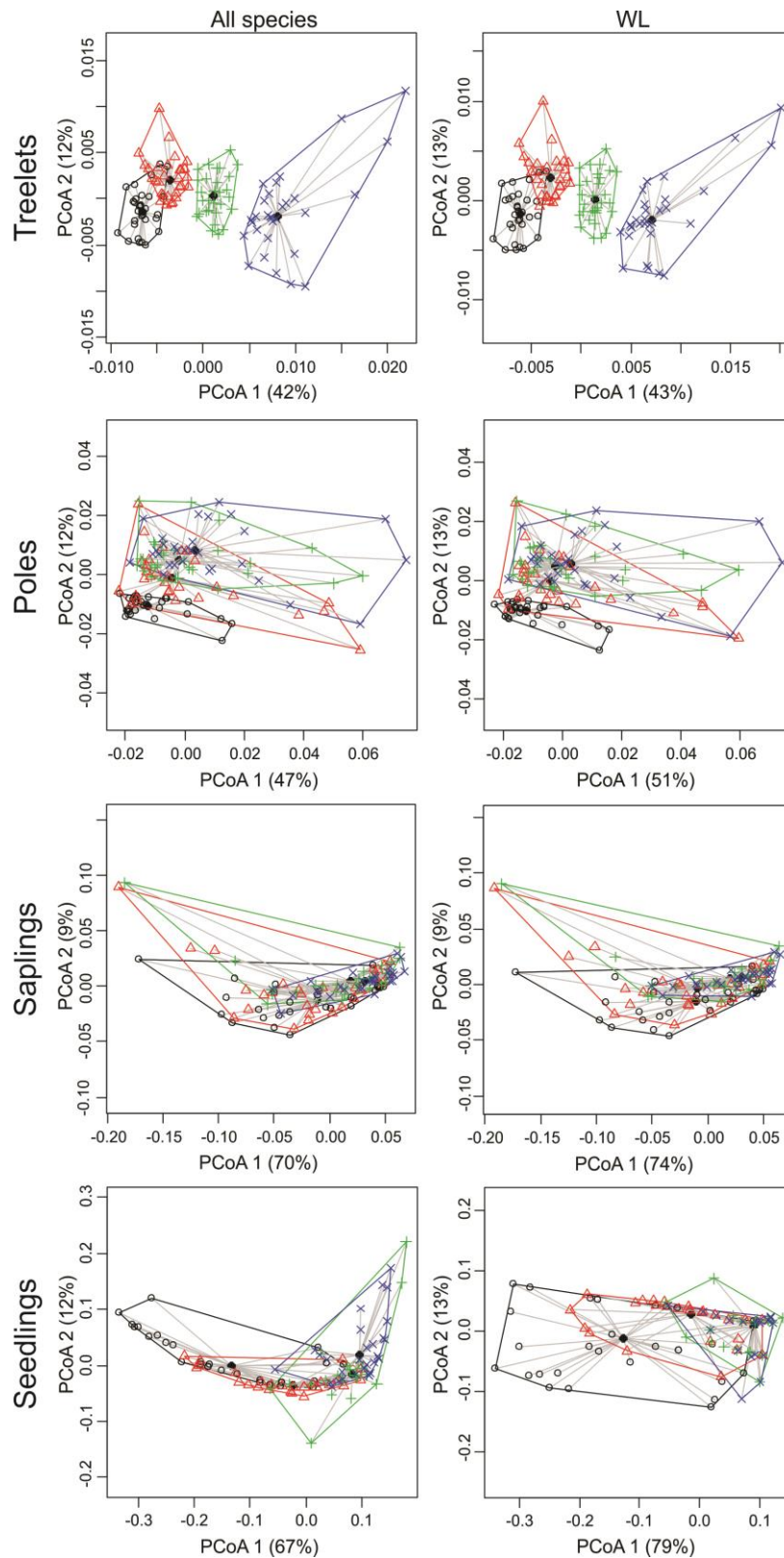
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Supplementary file 2 related to “Drought generates large, long-term changes in tree and liana regeneration in a monodominant Amazon forest” (B. S. Marimon, C. Oliveira-Santos, B. H. Marimon-Junior, F. Elias, E. A. de Oliveira, P. S. Morandi, N. C. C. dos S. Prestes, L. H. Mariano, O. R. Pereira, T. R. Feldpausch and O. L. Phillips)



Supplementary Fig. S.2 Average (and standard deviation) values of (A) MCWD (maximum climatological water deficit, mm year⁻¹) and (B) air temperature (°C) in four periods (P1: 1996-1997; P2: 1998-2002; P3: 2003-2010; P4: 2011-2018) before each census in a monodominant forest in Southern Amazonia. Different letters denote significant differences (Repeated-Measures PERMANOVA).

Supplementary file 3 related to “Drought generates large, long-term changes in tree and liana regeneration in a monodominant Amazon forest” (B. S. Marimon, C. Oliveira-Santos, B. H. Marimon-Junior, F. Elias, E. A. de Oliveira, P. S. Morandi, N. C. C. dos S. Prestes, L. H. Mariano, O. R. Pereira, T. R. Feldpausch and O. L. Phillips)



Supplementary Fig. S.3 Beta diversity of treelets, poles, saplings and seedlings over 21 years in a monodominant forest in Southern Amazonia. Principal coordinates (PCoA) biplots show the Euclidean distance between floristic composition assemblages within each survey. The black circles indicate group centroids, and lines, symbols and colors represented the minimum convex hulls around each group. Surveys: 1997 (black), 2002 (red), 2010 (green) and 2018 (blue). WL= without lianas.